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Research Article

Enteroparasitic fauna of non-native Chinook salmon (*Oncorhynchus tshawytscha*) on the Chilean coast: host-parasite networks and the potential for spillback

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Abstract

Invasive species can disrupt disease dynamics in new areas. Upon introduction, an invasive species in its new range may be colonised by novel parasites that normally infect native fauna. If the infected invasive host then helps to spread and boost the parasites to native hosts, this is known as spillback. Chinook salmon (*Oncorhynchus tshawytscha*) were released into rivers in southern Chile around 1924 and became invasive from 39°S to 53°S. Its anadromous migration and predatory behaviour involve multiple interactions with various native species. We examined the digestive tracts from 114 adult Chinook salmon returning from the sea to the estuary in the Toltén River, Chile to characterise their enteroparasite diversity, classify parasite developmental stages and assess Chinook's potential as a definitive host for local, native parasites. We enumerated 12,277 larvae of parasitic individuals belonging to the genera *Anisakis* and *Hysterothylacium* (Nematoda), *Nybelinia* (Cestoda) and orders Pseudophyllidea, Tetraphyllidea and Trypanorhyncha (Cestoda). Amongst these, we also found adults — one immature female, four gravid females and eight males of the nematode *Hysterothylacium* sp., six adults of the trematodes *Lecithaster* sp. and one *Lampritrema* sp. Finding advanced and adult stages suggests chinook are a competent non-native host for *Hysterothylacium*, *Lecithaster* and *Lampritrema*, as well as a non-native host for larval stages of *Nybelinia* sp., Pseudophyllidea and Tetraphyllidea. Our study demonstrates the integration of native parasites into an invasive host along the coast of Chile. Namely, Chinook salmon are now acting as a novel host that is positioned as a new node in trophic interactions and host-parasite networks. Additionally, our study provides valuable baseline data for further research on the impact of these parasites on native species and ecosystem dynamics, including the extent to which spillback is occurring.

Key words: Chinook salmon, coastal ecosystems, enteroparasites, invasive species, La Araucanía

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Introduction

Biological invasions represent one of the major threats to global biodiversity, profoundly altering the structure and functioning of natural ecosystems (Lymbery et al. 2014; Seebens et al. 2017). The introduction of invasive species can modify a wide range of ecological processes, from resource competition to trophic

interactions amongst native species (Byers 2000; Dick et al. 2010; Gehman and Byers 2017). In many cases, invasive species rapidly adapt to new environments, displacing or preying on local species, which leads to disruptions in the dynamics of trophic networks (Marcogliese 2002; Seebens et al. 2017). A common example is the introduction of fish or marine mammal species that compete with native species for limited food resources, which may result in a decline in native populations and alter the structure of communities (Ruggerone et al. 2023). In these cases, interspecific competition for food can lead to a reconfiguration of trophic networks, reducing the availability of prey for secondary consumers and even affecting species diversity within the ecosystem (Marcogliese 2002; Ruggerone et al. 2023). At the community level, invasive species can reshape fish, mollusc or algal assemblages, affecting not only feeding interactions, but also patterns of parasitism (Torchin et al. 2003; Wood et al. 2007; Dunn 2009; Dunn et al. 2012; Blakeslee et al. 2020). Invasive species can also act as vectors for new parasites, which, in the absence of natural predators or competitors in the new environment, proliferate unchecked (Kelly et al. 2009; Sarabeev et al. 2019; Verneau et al. 2025). Conversely, introduced species may acquire parasites from native species, transforming into a new host that adds additional parasitic load into the new ecosystem (Dunn 2009; Kelly et al. 2009). Therefore, the trophic networks of systems that harbour invasive species can be altered, along with the trophically transmitted host-parasite dynamics.

The introduction of invasive species into new habitats can trigger complex ecological effects, particularly in the dynamics of parasite transmission (Torchin et al. 2002, 2003; Dunn 2009; Verneau et al. 2025). When an invasive species establishes itself in a new ecosystem, it may acquire local parasites; some of these invasive species may, in fact, provide ideal conditions for the development and reproduction of native parasites (Kelly et al. 2009; Goedknegt et al. 2016; Byers 2021; Verneau et al. 2025). This phenomenon, known as spillback, occurs when parasites acquired by the invasive species develop and reproduce within it, releasing their propagules into the environment and increasing parasitic loads (prevalence and intensity of infection) in the native species within the ecosystem (Kelly et al. 2009; Goedknegt et al. 2016).

For example, the Pallas's squirrel *Callosciurus erythraeus* was introduced into Japan in the early 20th century. Several studies have reported that it not only hosts exotic ectoparasites, but also serves as a new host for native mites, fleas and ticks (Shinozaki et al. 2004; Katahira et al. 2022). *Callosciurus erythraeus* has become a competent host for native ectoparasites, facilitating the development of the parasites, allowing them to persist in the region and increasing the abundance of parasitic infections in native populations (Katahira et al. 2022). Furthermore, for parasites that are trophically transmitted, the accumulation of parasites in invasive species can boost their rates of transmission to native predators that feed on infected invaders (Marcogliese 2002; Medoc et al. 2017). Therefore, species invasions not only reconfigure the structure and functioning of ecosystems, but also affect parasitic communities, by increasing interaction nodes and making them more interconnected due to the transfer of parasites between species across different trophic levels.

Invasive species often alter predator-prey interactions, which are key drivers in many ecological and evolutionary processes (Freeman and Byers 2006; Dunn 2009; Dick et al. 2010; Gehman and Byers 2017; Ruggerone et al. 2023). Several studies have shown that, when native predators are given the choice between native and non-native prey, they tend to select the latter, driven by factors such

as avoiding conflicts with competitors or expanding their dietary breadth. Pintor and Byers (2015), through a meta-analysis, quantified the effects of non-native prey on native predator populations. Their results revealed a significant increase in predator abundance following the introduction of non-native prey, especially when the introduced prey were additive (and not substitutive) additions to the prey community. However, non-native prey not only become a new node within local food webs, but also can facilitate the transfer of parasites across different trophic levels. Invasive species can transmit parasites in their larval stage to native predatory definitive host species (Marcogliese 2002; Goedknegt et al. 2016). This occurs when invasive species serve as suitable hosts to accumulate larvae of trophically-transmitted parasites that develop in other definitive hosts. For example, in Australia, the invasive Cane toad (*Bufo marinus*) caused spillback by transmitting native parasites to local frog species. Two native frogs, the Green and Golden bell frog (*Litoria aurea*) and the Southern bell frog (*Litoria raniformis*), were affected by the spread and transmission of myxosporean parasites, which contributed to declines in their populations (Hartigan et al. 2011). This interaction can have considerable influences on the food-web topology (Medoc et al. 2017). This example shows that such a new trophic node in an invaded system would boost dynamics of an already existing parasite or propagate a novel parasite, broadening the host range and promoting parasite circulation within the food web. Therefore, invasive species not only alter the parasitic composition of the environment, but also modify the dynamics of parasite transfer between species, thus increasing the complexity of parasitic interactions within the food webs of the invaded ecosystem.

Amongst the most successful invasive species in aquatic environments are salmon, which are characterised by their high adaptability to variable environmental conditions, aggressive behaviour, exceptional mobility and generalist feeding plasticity (Soto 1997). Several studies have shown that the introduction of salmon damages ecosystems, primarily due to the high densities and large body sizes they attain in their new habitat. The absence of natural predators, favourable environmental conditions and abundant food sources are key factors that facilitate their rapid acclimatisation and development.

In southern Chile, the introduction of around 12 salmonid species has resulted in at least three successful invasions, with the Chinook salmon (*Oncorhynchus tshawytscha*) being the most recent to establish and form returning populations (i.e. those that return from the sea to spawn in their natal riverine habitat), with a distribution ranging from 39°S to 53°S in Chile and between 43°S and 54°S in Argentina (Soto et al. 2007; Correa and Gross 2008; Arismendi et al. 2014). Releases of Chinook salmon fry and juveniles date back to 1886 (Ibarra et al. 2011). In 1924, eggs of Chinook were imported from the United States and were sown in the river basins of Los Lagos Region (Soto et al. 2007) and the first returning adults were documented in 1979 in the same locations (Correa and Gross 2008).

Chinook salmon inhabit marine environments for three to six years before reaching sexual maturity (Ibarra et al. 2011; Gómez-Uchida 2016). In Chile's freshwater ecosystems, they primarily feed on benthic and terrestrial aquatic macroinvertebrates (Ibarra et al. 2011; Fierro et al. 2016; Bravo et al. 2019). In marine ecosystems, several studies conducted in Patagonia on returning Chinook salmon indicate that their diet is primarily composed of fish, along with some cephalopods (Niklitschek and Toledo 2011; Hüne et al. 2018). Therefore, given salmon's wide diet and given that parasite transmission mainly occurs through

trophic interactions, various parasite species may be infecting the Chinook salmon (Thieltges et al. 2013). In this context, parasitological studies on Chinook salmon have identified plerocercoids of *Dibothriocephalus latus* and *D. dendritticum*, larval nematodes such as *Camallanus corderoi*, *Anisakis* sp. and *Contracaecum* sp., adult digeneans such as *Derogenes lacustris* and acanthocephalans such as *Acanthocephalus tumescens* and *Corynosoma* sp., all of which have been found in juvenile salmon from Lake Panguipulli and from rivers of Patagonia (Ortubay 1994; Bravo 2005; Muñoz and Olmos 2008; Bravo et al. 2019; Rubilar et al. 2022). In a recent study, Figueroa-Muñoz et al. (2025) report only the abundance of the cestode *Hepatoxylon trichiuri* larvae in adult returning Chinook salmon from a river in Patagonia (Figueroa-Muñoz et al. 2025). Therefore, currently, there are no reports of enteroparasitic fauna in adult Chinook salmon returning from the sea. Given the predatory nature of Chinook, especially during both their freshwater and marine phases, it is crucial to investigate the native parasites it may acquire through trophic interactions and assess the impact of this introduction on the colonised ecosystems.

In this study, we quantify an introduced host species' parasite that are shared with native competitors and that also serve as indices of novel trophic interactions of the introduced host. Given that Chinook salmon have established, it is expected that the species might act as an intermediate host for larval parasites and a competent host for adult native parasites that inhabit the eastern Pacific Ocean in southern Chile. Ultimately our work provides a baseline for subsequent, important ecosystem questions such as how possibly new transmission pathways may affect ecosystem dynamics, including interactions between native species and their parasites. Paramount amongst these is the issue of spillback, i.e. do invasive species facilitate the spread of parasites in ways that would not occur in their absence? Such questions are critical to understanding the dynamics of parasitic infections in ecosystems harbouring invasive host species. Most helminth parasites rely on host feeding ecology for transmission and, given the extent of Chinook salmon invasion in Chile, we explore the fish's possible role facilitating the transfer of larval parasites to higher trophic levels through predation. To address this, we assessed the prevalence, abundance and richness of enteroparasites of returning Chinook salmon, from Caleta La Barra, Toltén, in the Araucanía Region.

Materials and methods

Study site and sample collection

The study was conducted at the mouth of the Toltén River ("La Barra"), located on the south-eastern Pacific coast of Chile (39.3503°S, 73.2230°W). Adult Chinook salmon (*Oncorhynchus tshawytscha*) returning from the ocean to the river were captured at this site, situated in the Araucanía Region. Sampling was carried out by artisanal fishermen from Caleta La Barra between early January and mid-February 2022. The collection of Chinook salmon is regulated by a fishing quota authorised exclusively by the Chilean National Fisheries and Aquaculture Service (Exempt Resolution 3261-2021, SERNAPESCA; Servicio Nacional de Pesca 2021), which permits capture only during specific months of the year. Additionally, it was not possible to obtain samples from other sites, as Caleta La Barra is the only coastal location currently authorised for Chinook salmon fishing at the river mouth. Further south, in regions such as Los Lagos and Aysén (Chilean Patagonia), fishing is only permitted in inland waters and only between October and January, starting in 2023 (Exempt Resolution 01-2023,

SERNAPESCA; Servicio Nacional de Pesca, 2023). This restriction limits legal sampling to that period and poses challenges for obtaining specimens during other seasons, as well as for assessing geographical variability in parasite distribution.

The digestive tracts were removed from 114 captured specimens provided by local fishermen for analysis. The digestive tracts were stored at -15 °C until further processing. Upon thawing, the tract ends were tied and the length of each tract was measured (cm). In addition, the sex of the host was determined, based on the presence or absence of gonads in the sample. That is, female gonads are sold by the fishermen; therefore, when digestive tracts arrived without gonads, they were classified as females. In contrast, digestive tracts corresponding to males always contained male gonads, allowing for clear identification of sex.

Laboratory sample processing and parasite identification

Once the samples were thawed in the laboratory, the digestive tracts were dissected longitudinally, from the oesophagus to the anus. Since the salmon were dissected at Caleta Toltén, where the musculature is sold for commercial purposes, only the digestive tracts were made available for analysis. As a result, it was not possible to examine the coelomic cavity prior to sample preservation and not all digestive tracts retained their mesenteries intact; therefore, mesenteric tissue was not included in the parasite examination. The intestinal mucosa was then carefully scraped and the material retained in the tract was extracted. The digestive contents were placed in Petri dishes with distilled water and examined under a stereomicroscope for the presence of parasites. Following Muñoz and Olmos (2008), the contents of each digestive tract were filtered using a porous sieve with a mesh size of 0.3 mm in diameter. At this stage, under stereoscope microscopy the helminth parasites were classified into three groups: nematodes, cestodes and digenean trematodes and collected.

The collected helminth parasites were preserved in 1.5 ml Eppendorf tubes, with some stored in 5% formalin and others in 96% ethanol, depending on the type of parasite. Subsequently, under stereoscopic magnification (4× and 10×), for each digestive tract, we identified and enumerated the parasites by taxa. Taxonomic identification of the parasites was done to the lowest possible level and based on the observation of their distinctive morphological features. For nematodes and digeneans, lactophenol of Amman and acetic carmine stain were used to clear the cuticles and internal structures, respectively. The following keys and reference guides were consulted for taxonomic identification: Anderson et al. (2009) for nematodes, Yamaguti (1959) for cestodes and Yamaguti (1971) for digeneans.

Data analysis

Parasitological descriptors, including prevalence, mean abundance and mean intensity of each parasite taxon, were calculated across all digestive tracts following the methodology of Bush et al. (1997). We also calculated the prevalence of all digestive tracts infected by at least one parasite taxon. First, we analysed the density of parasites (abundance of parasites /digestive tract length (cm)) as a function of sex, digestive tract length and their interaction using Ordinary Least Squares Regression (Zar 1984). In these models, the sex of Chinook salmon and digestive tract length were treated as fixed factors. Visual inspection of the residuals indicated that a Normal distribution was the most appropriate link function for the

parasite density model. To evaluate the goodness-of-fit of the parasite density model, the F-statistic was used to determine whether the independent variables (sex and digestive tract length) significantly explained the variability in parasite density. The coefficient of determination (R^2) was calculated to quantify the proportion of variability in parasite density explained by the model. Second, we used a generalised linear model (GLM) with a Poisson distribution to evaluate the relationship between parasite species richness in salmon as a function of salmon sex and gut length. Model goodness-of-fit was estimated using McFadden's pseudo-R^2, which allowed us to measure the amount of variation in parasite species richness explained by the independent variables. All statistical analyses were conducted in JMP 18.

Results

Of the 114 digestive tracts analysed, 55 were from males, with an average length of 58.7 cm (ranging from 42 to 71 cm), while 59 tracts were from females, with an average length of 62.6 cm (ranging from 48 to 75 cm). Amongst the analysed tracts (n = 114), 105 (92.1% of the total) were parasitised by at least one parasite taxon. Regarding larval parasites, specimens of the genera of nematodes, such as *Anisakis* and *Hysterothylacium*, were identified, as well as cestodes from the genus *Nybelinia* and from the orders Pseudophyllidea, Tetraphyllidea and Trypanorhyncha (Table 1). For adult parasites, nematodes from the genus *Hysterothylacium* and digeneans of the genera *Lecithaster* and *Lampritrema* were identified (Figs 1, 2). A total of 12,297 parasites were recorded, representing five genera and three orders, of which 12,277 (99.84%) were larvae and 20 (0.16%) were adult specimens. Of the 20 adults, 13 were identified as *Hysterothylacium* sp., including one immature female, four gravid females and eight males (Fig. 1, Table 1). The identification of adult individuals is based on the presence of developed male structures, such as the spicule and curved tail, as well as the occurrence of papillae in males. In females, the developed vulva and the presence of eggs are observed (Fig. 1). Six adults of *Lecithaster* sp. and one adult of *Lampritrema* sp. were also found (Fig. 2, Table 1). In the case of *Lecithaster* sp., reproductive structures such as testes and ovaries were observed (Fig. 2A). In contrast, the individual of *Lampritrema* sp. only exhibited the ovary (Fig. 2B).

Regarding parasitological descriptors, cestode Tetraphyllidea larvae exhibited the highest prevalence (72%), mean abundance and mean intensity amongst the identified parasites, followed by nematodes of *Hysterothylacium* sp., Pseudophyllidea plerocercoids, *Nybelinia* sp. cestode larvae, *Lecithaster* sp. digeneans, *Anisakis* sp. larvae and, finally, *Lampritrema* sp. and individuals from the order Trypanorhyncha (Table 1).

Density of parasites as a function of sex and length of digestive tract

The density of helminths parasites in a digestive tract ranged from 0–19.59 per cm. Sex did not significantly affect the density of helminths parasites ($p = 0.90$, Table 2). The least squares analysis revealed an inverse relationship between digestive tract length and parasite density: as the digestive tract length increased, parasite density decreased ($p < 0.002$, Table 2, Fig. 3). There was no significant interaction between sex and intestine length ($p = 0.81$). The R^2 value for the complete model was 0.07, indicating that sex and digestive tract length account for only 7% of the variability in parasite density. This relatively low value suggests that other factors not included in the model may significantly influence the variability in parasite density (Fig. 3).

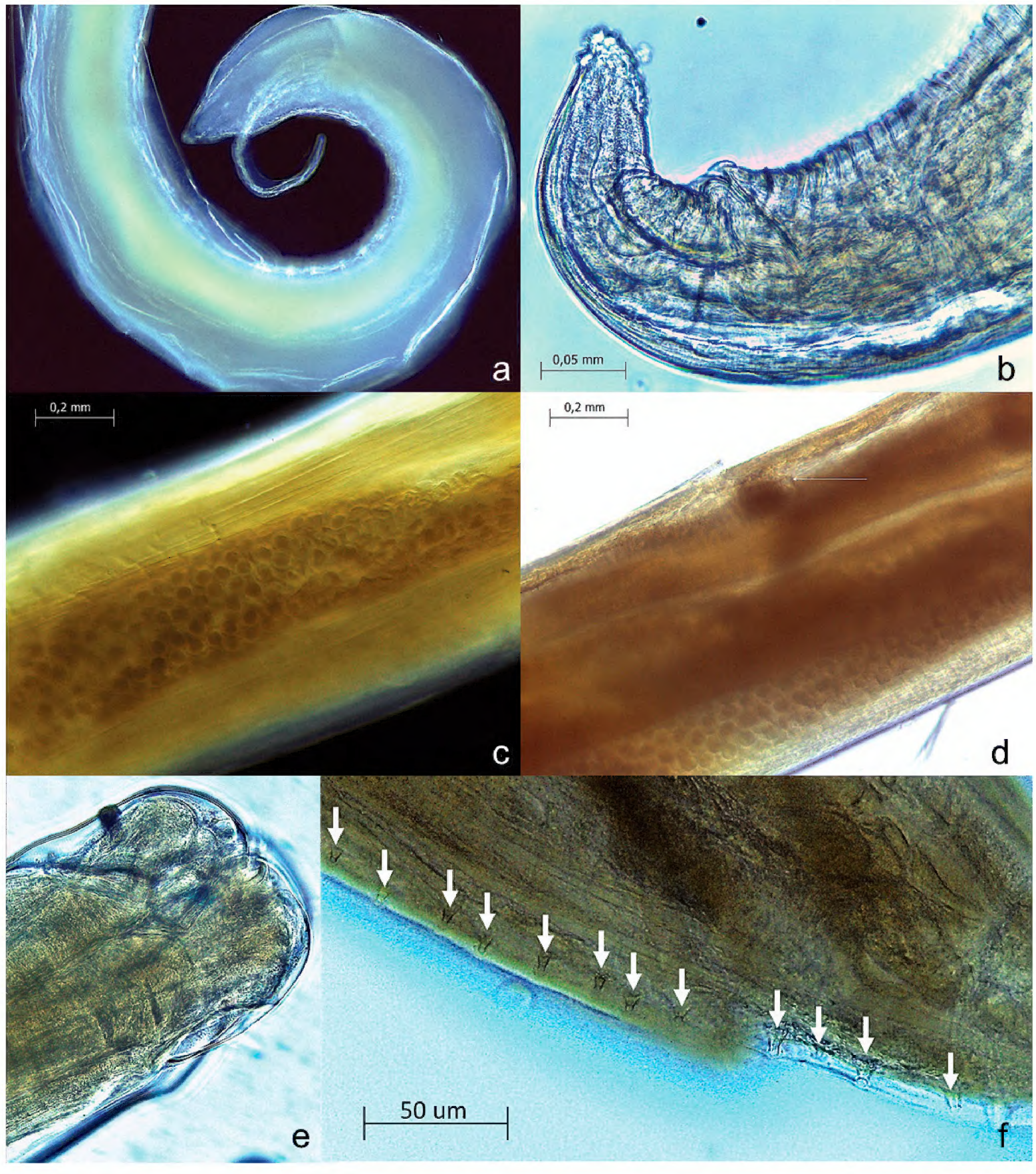

Figure 1. Adults of *Hysterothylacium* sp. **a.** Male tail and spicule; **b.** Curved male tail; **c.** Immature eggs of female; **d.** Vulva and mature eggs of female; **e.** Developed lips of adult; **f.** Male tail, with papillae indicated.

Table 1. Prevalence, mean abundance and mean intensity of the identified enteroparasitic fauna in 114 digestive tracts of Chinook salmon from the Chilean coast.

	Prevalence (%)	Mean abundance	Mean intensity
Nematoda			
Anisakis sp.	2.63	0.03	1.00
Hysterothylacium sp.	57.0	1.93	3.40
Trematoda			
Lampritrema sp.	0.88	0.01	1.00
Lecithaster sp.	2.63	0.05	2.00
Cestoda			
Nybelinia sp.	12.28	0.25	2.00
Pseudophyllidea	27,19	1.16	4.26
Tetraphyllidea	71.92	104.43	145.20
Trypanorhyncha	0.88	0.01	1.00

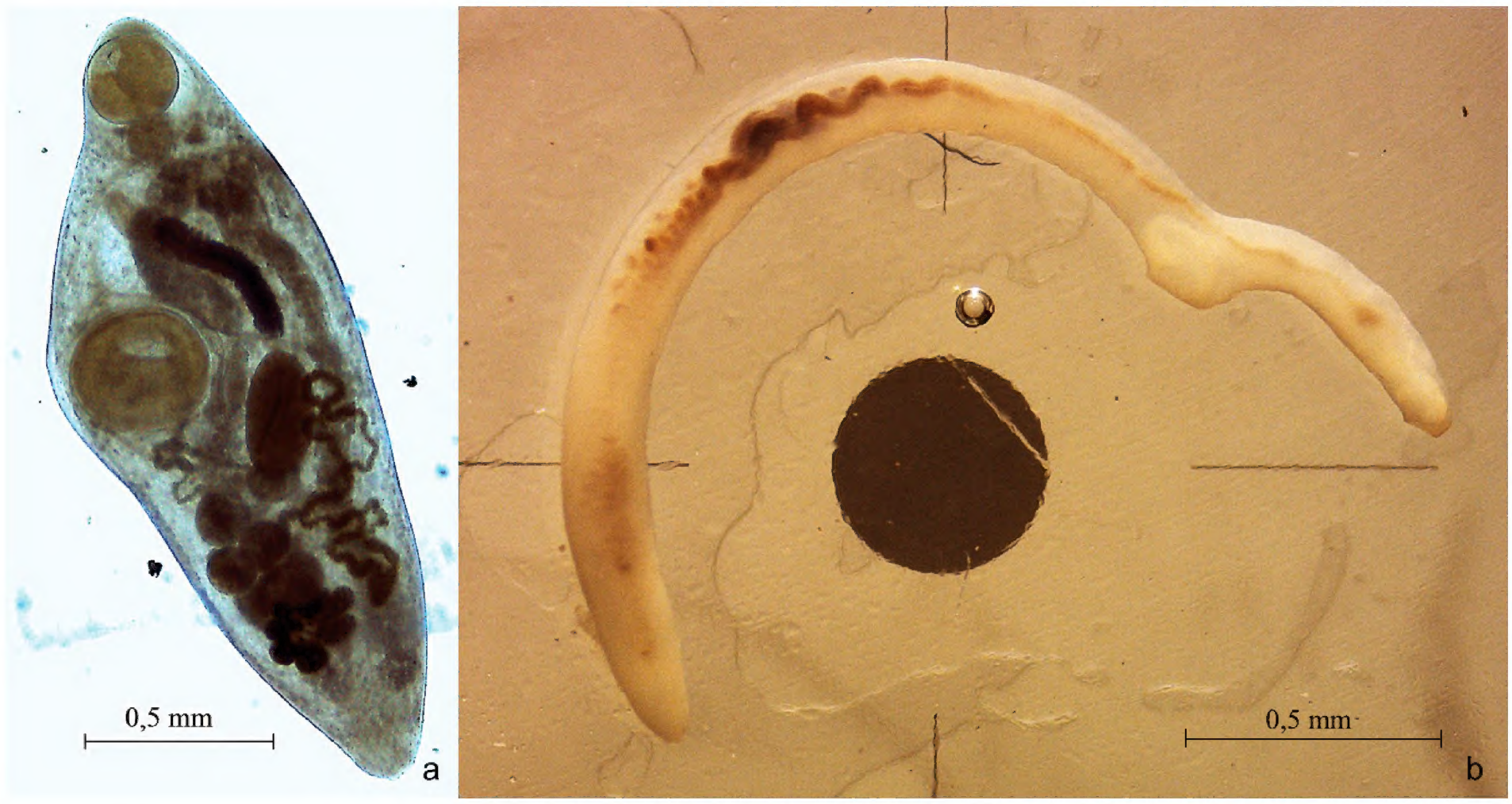

Figure 2. Adult specimen of *Lecithaster* sp. **(a)**, adult specimen of *Lampritrema* sp. **(b)**.

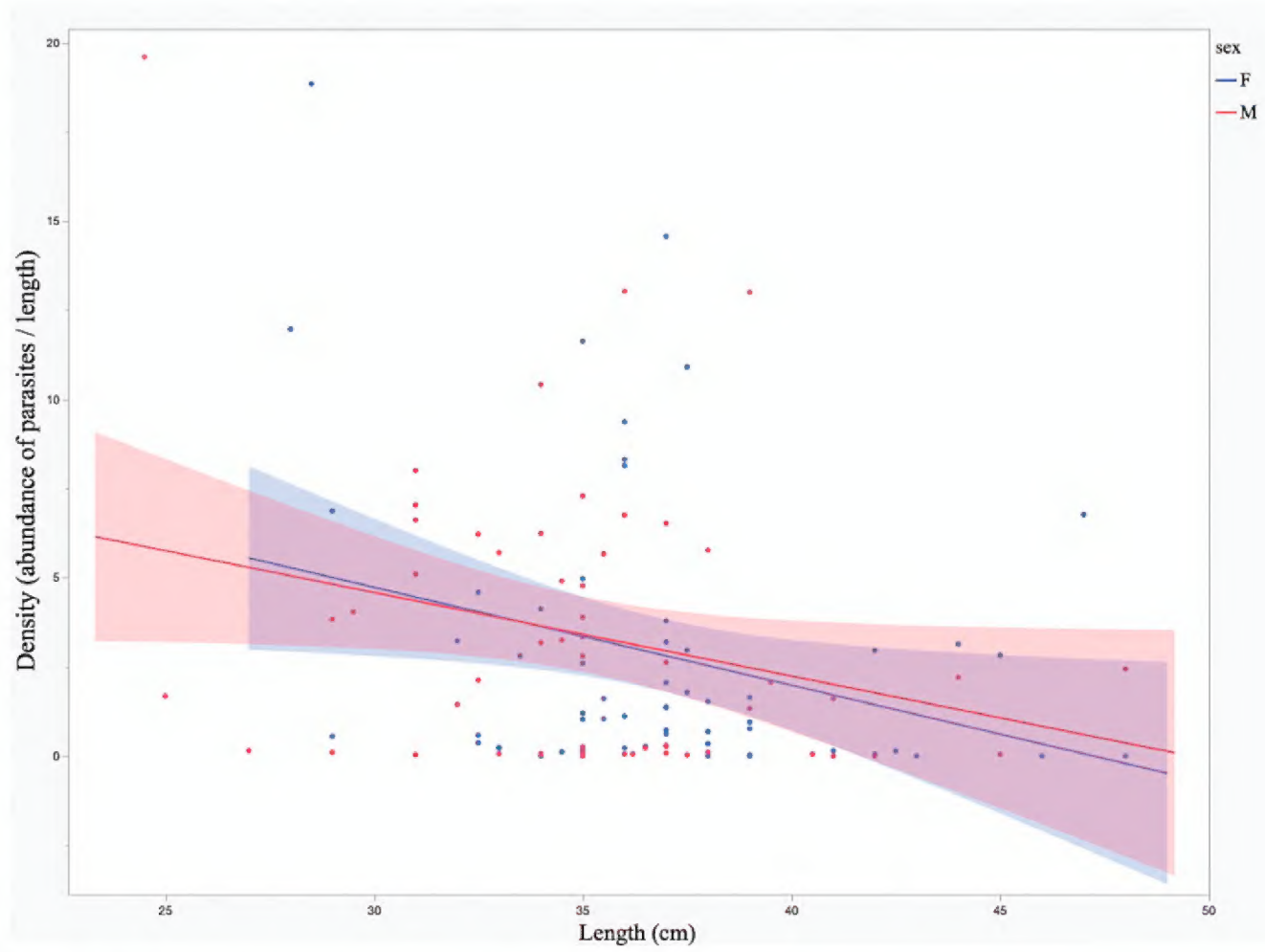

Figure 3. Density of parasites (abundance of parasites / tract length) in relation to the length of the digestive tract in 114 male and female Chinook salmon from southern Chile.

Richness of parasites as a function of sex and length of digestive tract

The average helminth parasites species richness in a digestive tract was 1.74 species (± 0.92). There were also no effects of sex ($p = 0.85$) nor intestine length ($p = 0.40$) on parasites species richness (Table 3, Fig. 4). There was no significant interaction of sex and digestive tract length on species richness ($p = 0.98$). The model fit was low, with a Pseudo R^2 of 0.0023. This indicates that the considered variables explain only 0.23% of the variation in parasite species richness.

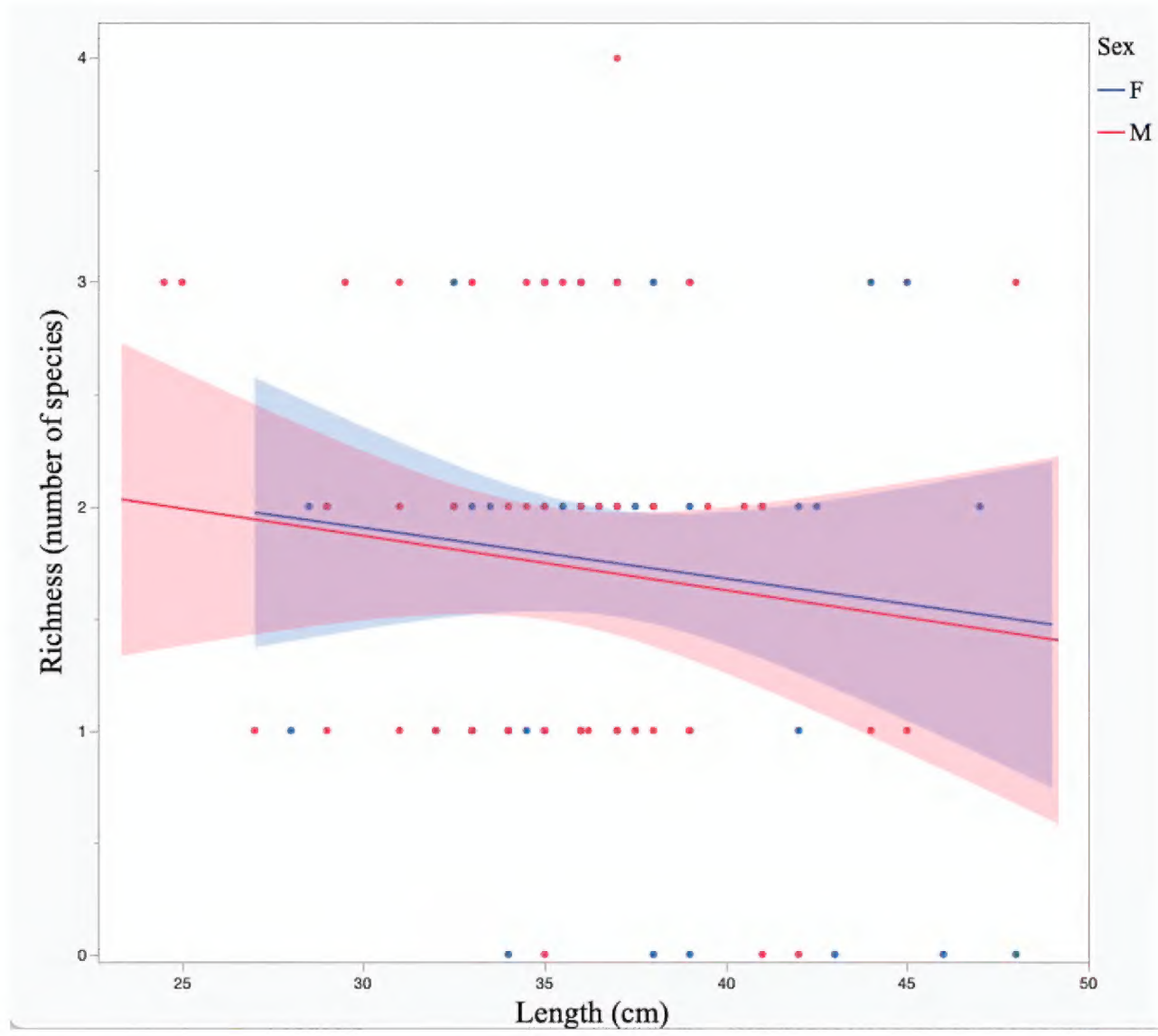

Figure 4. Parasite species richness as a function of the length of the digestive tract from 114 male and female Chinook salmon from southern Chile.

Table 2. Results of the least squares analysis examining the relationship between parasite density (parasite abundance per digestive tract length) and the fixed effects of sex and digestive tract length in Chinook salmon. The table includes estimates of effects, standard errors, t-statistics and p-values for each fixed effect term.

	Term	Estimate	Std. Error	t-value	*p*
Density of parasites	(Intercept)	12.282	3.030	4.05	< 0.0001
	Length	-0.254	0.083	-3.04	**< 0.002***
	Sex (M)	-0.047	0.037	-0.13	0.899
	Length × Sex	-0.020	0.083	-0.25	0.811

Discussion

This study revealed that Chinook salmon (*Oncorhynchus tshawytscha*) from the Toltén River Basin serve as a host for larval stages of the nematodes *Hysterothylacium* sp. and *Anisakis* sp., the cestode *Nybelinia* sp. and other cestode species from the orders Trypanorhyncha, Pseudophyllidea and Tetraphyllidea. Additionally, adult individuals of *Hysterothylacium* sp. and the digenean trematodes *Lecithaster* sp. and *Lampritrema* sp. were recorded, marking the first report of these native parasite species in Chinook salmon in Chile. The density of parasites decreased with increasing length of the analysed digestive tract. However, species richness did not show significant variation with respect to host sex or tract size. In the following discussion, we explore how, 46 years after the first report of returning adult salmon along the southern coast of Chile, Chinook salmon have emerged as a non-native intermediate host for various parasitic helminth species, some of which trophically transmit into higher trophic levels. It is important to note

Table 3. Results of GLM for the relationships of species richness as a function of sex and length of digestive tract of Chinook salmon. Estimate effects, their standard errors and *z*-statistic are provided for each fixed effect term.

	Term	Estimate	Std. Error	Z-value	*p*
Species richness	(Intercept)	1.044	0.588	3.143	0.076
	Length	-0.013	0.016	0.693	0.404
	Sex	0.013	0.072	0.033	0.854
	Length × Sex	0.000	0.016	0.000	0.978

that the earliest introductions of Chinook salmon to Chile, beginning in 1886, involved mainly fry and juvenile stages, with subsequent introductions of eggs in 1924. As these early life stages are unlikely to harbour adult parasites, it is plausible that the parasite fauna associated with Chinook salmon has established or been introduced progressively, alongside the development of self-sustaining salmon populations and the appearance of returning adults. Furthermore, in addition to the reported larval stages, we present the first documentation of native adult parasites in Chinook salmon, suggesting a potential spillback effect in the marine ecosystem along the Chilean coast.

Chinook salmon serve as an intermediate host for several species of larval parasites. These parasites first utilise marine invertebrates as primary hosts and, subsequently, the Chinook as an intermediate host, where they reach sexual maturity in marine mammals, birds and elasmobranchs (Muñoz and Olmos 2008). For instance, larvae of Pseudophyllidea parasitise native teleost species and salmon (Torres et al. 1990, 1991; Muñoz and Olmos 2008), maturing in marine birds or pinnipeds (Torres et al. 1993; Hinojosa-Sáez and González-Acuña 2005; Muñoz and Olmos 2008). Similarly, Tetraphyllidea larvae have been found in primary hosts such as bivalves, polychaetes and isopods (Carvajal 1977; Oliva et al. 1986; Sepúlveda et al. 2004; Oliva and Sánchez 2005), as well as in native fish and salmon (Torres et al. 2000; Muñoz and Olmos 2008), with adults reaching their final stage in elasmobranchs (Carvajal and Goldstein 1969; Carvajal 1974; Carvajal and Dailey 1975; Carvajal and Cattan 1978, 1985). In the case of Trypanorhyncha larvae, they parasitise teleost and pelagic fish (Carvajal and Cattan 1978; Muñoz & and Olmos 2008; Aparicio-Rizzo and Muñoz 2017), but have also been recorded in cephalopods (Pardo-Gandarillas et al. 2009). Meanwhile, the nematode *Anisakis* sp. is considered a generalist parasite and has been recorded in the Chilean coast parasitising pelagic and coastal fish in their larval stage (Muñoz and Olmos 2008), with whales, dolphins and orcas serving as definitive hosts (Sagua and Carvajal 1987; Sagua et al. 1987; Muñoz and Olmos 2008). These findings are consistent with the results of Schatz and Park (2021), who proposed that non-native species are more likely to acquire larval parasites from the colonised habitat, especially generalist parasites. While it is possible that Chinook salmon act as a dead-end host for larval parasites, becoming infected without transmitting the parasites to a definitive host to complete their life cycle, it seems more likely that Chinook salmon have emerged as a new intermediate and paratenic host for several native larval parasite species. These parasites are then transmitted to higher trophic levels through predation. In this capacity, Chinook salmon facilitate the transfer of these parasites, contributing to the expansion of parasitic interactions within the local trophic network.

Furthermore, our results indicate that Chinook salmon act as a new definitive host for three species of adult parasites. The nematode *Hysterothylacium* sp. and the digeneans *Lecithaster* sp. and *Lampritrema* sp. displayed developed sexual structures, suggesting their sexual maturity within the intestine of the analysed salmon. These parasites, native to the region, have been reported in their adult stages in freshwater and marine fish, intertidal and pelagic native species along the Chilean coast (Figueroa and Puga 1991; Muñoz et al. 2017, 2018), as well as in farmed salmon (González 1998), which become infected through predation on invertebrates, primarily Gammaridae and polychaetes, that harbour the larval stages (González 1998). Although we were unable to perform molecular analyses due to funding limitations, all taxonomic identifications were conducted using well-established and widely accepted morphological keys (Yamaguti 1959, 1971; Anderson et al. 2009). We acknowledge that some diagnostic features used for adult nematodes, particularly in the genus *Hysterothylacium*, may overlap with those of other anisakids. However, our identifications were based on a detailed examination of morphological characteristics observable under stereomicroscopy and followed standardised diagnostic criteria as described in the cited taxonomic references. Moreover, representative specimens were preserved in 96% ethanol to enable future molecular analyses, which will help refine taxonomic resolution, particularly for cryptic taxa. Nevertheless, prevalences and abundances in native hosts (Figueroa and Puga 1991; Muñoz et al. 2018) are higher compared to the results obtained in this study. For example, for *Hysterothylacium* sp. previous studies report prevalences in native hosts of up to 80–90% with mean abundances exceeding 20–30 larvae per individual (Figueroa and Puga 1991; Muñoz et al. 2018), whereas in our study, the prevalence was 57% and the mean abundance was 1.93 parasites per Chinook, representing an approximate reduction of 29–37% in prevalence and about 90–94% in mean abundance. These findings align with previous studies suggesting that introduced species typically harbour fewer parasites than native species (Torchin et al. 2003). The arrival of Chinook to a new range and the acquisition of native parasites, followed by their development into adults within the invasive host, represents a key precursor for the spillback effect to occur (Dunn 2009; Kelly et al. 2009; Goedknegt et al. 2016).

In recent years, various studies have explored the implications of invasive species and the transport or acquisition of parasites in the habitats they colonise. Although Chinook may be considered a competent host for these adult parasites, the presence of eggs in the female parasites alone is not sufficient evidence to confirm that spillback is occurring in the native fauna. These eggs must spread into the environment and become infective to intermediate hosts, enabling their transfer to definitive hosts and the subsequent return to adulthood (de Castro and Bolker 2005; Dunn 2009; Kelly et al. 2009). In an extreme case, it is possible that salmon serving as hosts could lead to a dilution effect, which can occur when an invasive species acquires native parasites that originally affected native species (Dunn 2009; Kelly et al. 2009; Medoc et al. 2017). In these situations, the invasive species is not a suitable or competent host and it becomes a sink for these parasites that are unable to survive or reproduce efficiently in it. As a result, the non-native host absorbs parasites from the environment and the parasite load decreases in native hosts (Goedknegt et al. 2016; Blakeslee et al. 2020; Llopis-Belenguer et al. 2020). However, with the Chinook salmon, although they host fewer parasites compared to native species, its role as a definitive host for these parasites

implies the release of new propagules into the environment. This release could alter the parasitic load in the marine ecosystems of southern Chile, as native parasites could be transmitted through trophic interactions, affecting local fauna and introducing new flows of parasitism into the food web.

Invasive Chinook salmon have emerged as a new node within the food webs of ecosystems previously dominated by native fish species, likely altering not only predator-prey interactions, but also the parasitism dynamics in the ecosystem. This salmon harbours three species of parasites in their adult stage, acting as the definitive host and six species in their larval stage, which, through predation, reach their definitive hosts: elasmobranchs, pinnipeds and seabirds (Carvajal 1974; Torres et al. 1993; Muñoz and Olmos 2008). By integrating into the trophic flow, the salmon not only introduces new propagules (eggs of adult parasites) into the environment, but also becomes a trophic pathway that facilitates the transmission of native parasites to its predators (Dunn 2009; Kelly et al. 2009; Goedknegt et al. 2016). This phenomenon has a direct impact on the connectivity of the food web: incorporating salmon as an additional prey item not only increases the number of links in the network, but also redistributes parasitic interactions to higher trophic levels (Lafferty et al. 2006, 2008; Thieltges et al. 2009; Byers 2009). If this invasive salmon were considered as part of the network, the web would become denser, as the inclusion of parasites would increase the connections between nodes, altering the overall structure of the food web (Lafferty et al. 2006, 2008; Thieltges et al. 2009; Llopis-Belenguer et al. 2020). At the same time, this change in the network structure could have implications for the ecosystem's stability, as the increased connectivity, derived from the expansion of trophic interactions via parasites, could either strengthen or weaken the network depending on how these interactions are distributed (Lafferty et al. 2006, 2008; Goedknegt et al. 2016). For instance, the predators of the salmon not only acquire nutrients from the fish as prey, but are also affected by the parasites it carries, creating new links within the network. This shift in connectivity between species highlights the importance of including parasites in food web models, as their presence modifies interactions and can alter the dynamics of ecological stability (Lafferty et al. 2006, 2008; Byers 2009; Thieltges et al. 2013; Llopis-Belenguer et al. 2020). Therefore, the incorporation of Chinook salmon increases the connectivity of the food web and re-defines parasitic transmission patterns, reflecting how invasive species can transform the structure and stability of ecosystems, not only through their direct interactions, but also by altering the energy flows and parasitic links throughout the network.

The density of parasites decreased as the length of the digestive tract increased in both sexes. In this study, the length of the Chinook's digestive tract was used as a proxy for the total body length of the individual. While several previous studies have shown that, as the total fish length increases, both density of parasites and species richness also tend to increase (Flores and George-Nascimento 2009; Muñoz-Muga and Muñoz 2010), our results contrast with this general trend. This discrepancy may be attributed to the fact that only enteric parasites, i.e. those residing in the digestive tract, were analysed in this study, excluding parasites found in the coelomic cavity and mesenteries. Given that Chinook salmon serve as an intermediate host for a variety of parasites, one might expect to find additional parasites in the coelomic cavity and musculature, which were not considered in this analysis. In addition, there are two effects related to the fact that our analyses focused on adult salmon returning to spawn. The first is that the size of the salmon is skewed towards the larger end and would not include smaller individuals.

The truncated size distribution could make the effect of size harder to see relative to other studies of salmon that used a larger size range. Second, the observed decrease in parasite density with increasing digestive tract length could be related to the fasting process that returning salmon undergo prior to migrating to freshwater as mature adults (Bowerman et al. 2017). Fasting is a natural condition in the salmon lifecycle, during which they cease feeding and rely on energy reserves to migrate upstream, undergo gonadal maturation and meet other energy demands (Navarro and Gutiérrez 1995; Araya et al. 2014; Bowerman et al. 2017; Araújo et al. 2022). Specifically, fasting in salmon can last for several months before migration begins (Bowerman et al. 2017; Araújo et al. 2022). During this period of food deprivation, salmon not only stop acquiring parasites through trophic transmission, but also cease accumulating parasites. Consequently, while salmon continue to grow and mature, their lack of feeding leads to a decrease in parasite abundance. Along with this, salmon may expel parasites due to the aging of adult parasites within the digestive tract. Although little is known about the exact duration and longevity of parasites in their hosts, studies have estimated that nematodes and digeneans can reside in the host for 60 to 90 days (George-Nascimento 1991; Rodríguez and George-Nascimento 2021). After this period, it is plausible that many of these parasites are expelled into the environment through the salmon's faeces.

One of the main limitations of this study is the restricted temporal and geographical scope of sampling. Specimens were collected only during the summer months (January to mid-February; Exempt Resolution 3261-2021) due to legal constraints linked to a regulated fishing quota authorised by SERNAPESCA. This limited period prevents assessment of seasonal variation in parasite prevalence and intensity. Sampling was also restricted to a single coastal site — Caleta La Barra at the mouth of the Toltén River — currently the only authorised location in southern Chile for Chinook salmon capture at river mouths. In other southern regions, fishing is permitted only in inland waters and during specific months (October to January, Exempt Resolution 01-2023), limiting spatial coverage and the ability to evaluate geographic variability. Although Chinook salmon is a non-native species, its capture is strictly regulated, complicating long-term or large-scale parasitological studies. Additionally, the absence of molecular confirmation may limit taxonomic resolution for some cryptic taxa. Nonetheless, we minimised this limitation by applying detailed morphological examination using established taxonomic keys and preserved specimens for future genetic analysis once resources are available. Future research should seek closer coordination with regulatory agencies to enable broader and more flexible sampling. Expanding legal access to specimens across space and time would improve the ecological representativeness of the data and allow a better understanding of the Chinook's role in transmitting native parasites in Chilean aquatic ecosystems, which is crucial for effective management.

Conclusions

This study highlights the role of the invasive Chinook salmon (*Oncorhynchus tshawytscha*) as a non-native host within the trophic networks of southern Chile's marine ecosystems. Chinook salmon serve as a host for both larval and adult stages of native parasites, including species of *Hysterothylacium*, *Anisakis*, *Nybelinia*, *Lecithaster* and *Lampritrema*. By acting as an intermediate host for these parasites, the salmon likely facilitates the transfer of parasitic species to higher trophic levels, contributing to the

expansion of parasitic interactions within the food web. Moreover, the salmon's role as a confirmed definitive host for three species of adult parasites further complicates the dynamics of parasitism in these ecosystems. On one hand, this phenomenon may lead to spillback, potentially altering the natural parasite load and impacting native fauna. On the other hand, although Chinook salmon harbours fewer parasites compared to native species, its presence could be contributing to a dilution effect within the habitat. Nevertheless, its presence in the ecosystem broadens the host range for parasitic interactions, thereby increasing trophic connectivity and reshaping the structure of the food web. Consequently, the introduction of this invasive species has broader implications for ecosystem stability, as changes in parasitic dynamics could either strengthen or weaken the food web, depending on the distribution of these interactions. This study provides baseline data on the identity of helminths parasites and their infection prevalence and intensity in a widespread, non-native host. Our findings underscore the need to consider invasive species and their role in the transmission of parasites when assessing the ecological health and stability of marine ecosystems.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Use of AI

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Abundance of enteroparasites of chinook. Sex and digestive length

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Data type: numbers

Explanation note: The abundance of each parasite taxon found in the digestive tract of returning male and female salmon from Caleta Tolten, La Araucanía, Chile, is reported.

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